



A NEW SPECIES OF *RHIPIDOMYS* (RODENTIA, MUROIDEA) FROM NORTH-EASTERN BRAZIL ¹

(With 7 figures)

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ABSTRACT – The collections of mammals made in the 1950s by the Serviço Nacional de Peste (National Plague Service) in north-eastern Brazil include some 240 specimens of climbing mice, genus *Rhipidomys*, from the states of Ceará and Pernambuco. Morphological and morphometric analyses reveal the presence among them of a new species, *Rhipidomys cariri* sp.nov., described herein with two subspecies, namely the nominotypical subspecies and *R. cariri baturiteensis* ssp.nov., respectively from the mesic enclaves of Cariri and Baturité within the semi-arid caatinga of Ceará. The species may be distinguished from both the population of *R. mastacalis* found in eastern Pernambuco and that of *R. macrurus* occurring in the Serra de Ibiapaba on the western border of Ceará through its larger body size, greyer and coarser pelage, longer vibrissae and larger molars. Although the separation of the enclaves from the Atlantic forest to the east and the Amazonian forest to the west probably dates back only to the mid-Holocene or late Pleistocene, the new endemic species may well have a much more remote origin; molecular data would be needed to test this hypothesis.

Key words: Ceará, morphology, morphometrics, mesic enclaves, caatinga.

RESUMO – Uma nova espécie de *Rhipidomys* (Rodentia, Muroidea) do Nordeste brasileiro.

O material mastozoológico coletado no Nordeste pelo Serviço Nacional de Peste, na década de 1950, inclui cerca de 240 exemplares de ratos arborícolas do gênero *Rhipidomys* provenientes do Ceará e de Pernambuco. A utilização de métodos morfológicos e morfométricos permitiu distinguir entre eles uma nova espécie, *R. cariri* sp.nov., descrita aqui com duas subespécies, a nominotípica e *R. cariri baturiteensis* ssp.nov., respectivamente provenientes dos brejos (zonas úmidas) do Cariri e de Baturité, isolados na caatinga do Ceará. A espécie se distingue tanto da população de *R. mastacalis* encontrada no leste de Pernambuco quanto daquela de *R. macrurus* que ocorre na Serra de Ibiapaba, no extremo ocidental do Ceará, pelo seu tamanho corporal maior, sua pelagem mais cinzenta e menos lisa, suas vibrissas mais compridas e sua série molar maior. Apesar de a separação entre os brejos cearenses e a mata atlântica, ao leste, e a amazônica, ao oeste, remontar apenas até o meio do Holoceno ou o final do Pleistoceno, é possível que a nova espécie endêmica tenha origem bem mais antiga, hipótese esta que poderia ser testada com dados moleculares.

Palavras-chave: Ceará, morfologia, morfometria, brejos, caatinga.

INTRODUCTION

Mice of the muroid genus *Rhipidomys* Tschudi, 1845 are among the lesser known arboreal mammals of the Neotropics, yet they are widespread in South America. The twenty or more recognisable species inhabit most types of wooded habitat north of latitude 24°S, from rainforest to semi-deciduous woodland, as well as plantations and even the

rafters of rural dwellings. In Brazil they are found from Roraima to São Paulo and from Pernambuco to Acre (TRIBE, 1996).

In his book on the rodents of Brazil (MOOJEN, 1952), João Moojen listed four species of *Rhipidomys* from Brazil: *R. maculipes* (Pictet & Pictet, 1844), distributed in the 'matas do sul da Bahia. Ilhéus' ('forests of southern Bahia. Ilhéus'); *R. macrurus* (Gervais, 1855), found in northern

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Goiás; *R. mastacalis* (Lund, 1840), in the states of Minas Gerais and Rio de Janeiro; and *R. cearanus* Thomas, 1910, in the State of Ceará. Apart from very brief notes on their coloration and a table of measurements of the type specimens, he gave no indication as to how these forms might be distinguished other than geographically. Moojen's book was written, however, before he could see the full results of the collections of rodents made by the Serviço Nacional de Peste (SNP – the National Plague Service) in north-eastern Brazil, which were conducted under his overall direction mostly between 1951 and 1956 (OLIVEIRA & FRANCO, this volume). Examination of the hundreds of *Rhipidomys* specimens contained in these collections reveals that the pattern of species in north-eastern Brazil is more complex than Moojen's book suggested (CERQUEIRA, VIEIRA & SALLES, 1989). Indeed, a new species with two subspecies based on SNP material is described below.

MATERIAL AND METHODS

LOCALITIES AND SPECIMENS

The 1st Region (*1ª Circunscrição*) of the Serviço Nacional de Peste covered the four states of Ceará, Paraíba, Pernambuco and Alagoas, located north of the São Francisco river in north-eastern Brazil. Most of the area lies within the *polígono das secas* or drought zone, characterised by irregular, infrequent rainfall and covered mainly by the thorn scrub vegetation known as *caatinga*. Within the *caatinga*, ranges of hills and isolated massifs that intercept moisture-bearing winds provide more mesic habitats, known locally as *brejos*, which support mesophytic forests. A relatively narrow strip along the east coast receives high rainfall; this is the *zona da mata* or forest zone, originally covered by the northern end of the Atlantic forest but now almost entirely devoted to intensive farming. A band known as the *agreste*, originally occupied by semi-deciduous forest, buffers the *zona da mata* from the *caatinga*.

Within this region, *Rhipidomys* specimens were collected in the moister parts but not in the *caatinga* proper. Substantial series were obtained in four areas:

a) Crato (07°14'S 39°23'W), in the Cariri *brejo* of southern Ceará, where 24 *Rhipidomys cariri cariri* ssp.nov. are known to have been collected by the SNP in July-August 1946 and between July 1952 and April 1953. Freitas refers to 21 '*Holochilus*

sciureus' (see the species description for discussion of this misidentification), but does not include four specimens collected in a preliminary survey in 1946 (FREITAS, 1957, Tab.1).

b) Pacoti (04°13'S 38°56'W), in the Serra de Baturité *brejo* in northern Ceará, where 17 *Rhipidomys cariri baturiteensis* ssp.nov. were captured between July 1953 and November 1954. Freitas mentions 22 *R. cearanus* from Baturité district (FREITAS, 1957).

c) the Serra de Ibiapaba, western Ceará, especially at São Benedito (04°03'S 40°53'W) and Guaraciaba do Norte (04°10'S 40°46'W); 141 specimens of *Rhipidomys macrurus* are known to have been collected here between August 1952 and June 1954. Freitas, however, refers to 292 *R. cearanus* from the corresponding SNP district of Ipu (FREITAS, 1957); this number may include discarded and/or misidentified specimens. The hamlet of São Paulo in the Serra de Ibiapaba is the type locality of *R. cearanus* Thomas, regarded here as a junior synonym of *R. macrurus*.

d) the area of Caruaru (08°17'S 35°58'W), in eastern Pernambuco, where 58 *Rhipidomys mastacalis* were caught between April 1952 and November 1953. In addition, one *R. mastacalis* was taken at Garanhuns in eastern Pernambuco (08°54'S 36°29'W) in October 1952, and one at Anádia in Alagoas (09°42'S 36°18'W) in July 1955. Freitas lists 120 *R. mastacalis* from Caruaru and 5 from Garanhuns, but the Anádia specimen, which was marked as 'unidentified rat' on its record card, is not mentioned (FREITAS, 1957). For the purposes of analysis, the Anádia and Garanhuns specimens were included with the Caruaru series on the basis of morphological similarity and geographical proximity. All but three of the 242 specimens located are now in the collections of the Museu Nacional, Rio de Janeiro (MN), mostly in the form of study skins with cleaned skulls; the University of Kansas Natural History Museum (KU) has one and the National Museum of Natural History, Washington, D.C. (USNM) two specimens of *R. c. cariri* from Crato. The SNP material includes most of the *Rhipidomys* specimens known from north-eastern Brazil, relatively few individuals having been collected in the region before or since. This material was studied by the author as part of a broader investigation into the whole genus (TRIBE, 1996). References to *R. macrurus* and *R. mastacalis* in the following sections denote only the samples and populations mentioned above unless the context requires a more comprehensive interpretation.

ANALYSES

Specimens were examined and compared for the size and proportions of external, cranial and dental characters and for pelage colour and texture. External measurements recorded on specimen labels were accepted as approximations to the true values unless clearly in error; hind foot length was usually rechecked on the dry foot where possible. Specimens were allocated to dental age classes on the basis of their molar wear (see TRIBE, 1996, for details). Juveniles (those in which wear had not yet exposed the dentine in the lophs of the upper second molar) and old individuals (those in which the main enamel features of the M2 occlusal surface had been obliterated) were excluded from morphometric analyses, leaving 107 adults in classes 2-4 (11 *R. c. cariri*, 7 *R. c. baturiteensis*, 67 *R. macrurus* and 27 *R. mastacalis*). For the multivariate analysis, four of these *R. macrurus* specimens and one *R. mastacalis* for which missing values could not be imputed satisfactorily (TRIBE, 1996) were omitted from the adult dataset.

The following 30 skull dimensions were measured (see TRIBE, 1996, for definitions of measurement end points): occipito-nasal length (ONL); condylo-incisive length (CIL); palatal length (PL); post-palatal length (PPL); upper molar row – crown length (MRC); upper molar row – alveolar length (MRA); 1st upper molar breadth (M1B); palatal bridge length (PBL); temporal fossa length (TFL); diastema length (DL); incisive foramen length (IFL); incisive foramen breadth (IFB); palatal breadth at M1 (PB1); palatal breadth at M3 (PB3); mesopterygoid fossa breadth (MFB); breadth across incisor tips (BIT); bullar width (BW); bullar length (BL); braincase breadth (BCB); skull height (SH); rostral height (RH); rostral breadth (RB); rostral length (RL); nasal length (NL); zygomatic plate length (ZPL); interorbital breadth (IOB); zygomatic breadth (ZB); greatest length of mandible (GLM); mandibular molar row – alveolar length (MMR); depth of mandibular ramus (DR).

For each of the four taxa, descriptive statistics (range, mean and standard deviation) were calculated for each variable and for a number of bivariate ratios of interest. Student's *t*-tests were used to compare these means for each pair of taxa. Principal components analysis (PCA) was performed to provide a low-dimensional representation of the data (REYMENT, BLACKITH & CAMPBELL, 1984). PCA was chosen since it

does not impose any *a priori* structure on the data; that is, the specimens are not analysed according to their geographical groups of origin, as would be necessary with techniques such as discriminant analysis or MANOVA. The appearance in the results of any groupings congruent with the geographical origin of the specimens would thus demonstrate that the samples were morphometrically distinct along at least one major axis of variation of the pooled data. This would support the four-taxon arrangement described above on the basis of morphology and geographical origin.

In PCA, linear combinations (components) of the original variables are calculated sequentially so as to be uncorrelated with each other and to maximise the variance they contain; thus the major part of the variation present in all the original variables is expressed in a small number of components. The individual measurement values for a specimen (log-transformed and standardised) are multiplied by the coefficients that make up the latent vector (eigenvector) corresponding to each component, and the products are summed to produce a score for the specimen on that component. Bicomponent plots of the resulting specimen scores can then be examined in the light of groupings based on parameters such as sex, age or, as here, geographical provenance. In most cases, the first component in PCAs performed on vertebrate specimens predominantly represents variation in general specimen 'size' (REYMENT, BLACKITH & CAMPBELL, 1986), a large proportion of which will be of ontogenetic origin. The variation in 'shape' reflected in subsequent components is often more informative for phylogenetic purposes.

Since the number of specimens analysed must always exceed the number of variables (REYMENT, BLACKITH & CAMPBELL, 1984), a reduced set of 15 variables (PL, MRC, PBL, TFL, PB1, MFB, BW, BCB, SH, RB, NL, ZPL, IOB, MMR and DR) was used in PCAs involving fewer than 30 specimens, the dimensions excluded being those previously found to display the highest measurement errors or greatest sexual or ontogenetic variation among adults (TRIBE, 1996). Principal components are specific to the samples analysed and will change when specimens are added to or subtracted from the dataset (NEFF & MARCUS, 1980); the latent vector weightings therefore have to be interpreted anew for each subset of specimens analysed separately.

RESULTS

Morphologically, each of the four series of SNP specimens – *R. c. cariri* ssp.nov., *R. c. baturiteensis* ssp.nov., *R. macrurus* and *R. mastacalis* – was relatively homogeneous and there was no evidence from visual examination or univariate analyses of measurements (such as clear bimodality in distributions) to suggest that more than one taxon might be present in each sample. On the basis of specimen size and pelage, the four series fell clearly into two groups. The two separated by the greatest distance, *R. macrurus* and *R. mastacalis*, resembled each other in their moderate size and in their sleek, reddish-brown dorsal pelage with only a slight agouti effect. In contrast, *R. c. cariri* and *R. c. baturiteensis* were larger, with coarser, duller, more agouti pelage. No single variable or bivariate ratio provided unambiguous separation of the four series, since the ranges of values for the different taxa always overlapped. The *t*-test results, however, showed that the sample means for many variables were significantly different, several with a probability $p < 0.001$ of falsely rejecting the null hypothesis of equality of population means (see table 1 for a selection of significant variables and ratios). In the pairwise comparisons, the variable means that differentiated *R. c. cariri* and *R. c. baturiteensis* on the one hand from *R. macrurus* and *R. mastacalis* on the

other, with a probability $p < 0.05$, were MRC, MRA, TFL, BW, BL, RB, RL and DR. *Rhipidomys c. cariri* and *R. c. baturiteensis* had the larger means in each case. A number of bivariate ratios also had distinct means, including RL/ONL (rostral length as a proportion of skull length, greater in *R. c. cariri* and *R. c. baturiteensis*), RH/RL (relative height of the rostrum, shallower in *R. c. cariri* and *R. c. baturiteensis*) and PBL/MRC (relative length of the palatal bridge to the molar row, shorter in *R. c. cariri* and *R. c. baturiteensis*). Several other individual variables and bivariate ratios had means that distinguished either *R. c. cariri* or *R. c. baturiteensis* from both *R. macrurus* and *R. mastacalis*: ONL, CIL, PPL, PB1, MFB, ZB, GLM, PB1/PBL and BW/BCB were all larger in *R. c. cariri*; and DL, BCB, ZPL, MMR and IFB/IFL were all larger in *R. c. baturiteensis*.

The *R. c. cariri* and *R. c. baturiteensis* samples also differed from each other in several of these characters. Molar lengths and breadth were significantly greater in *R. c. baturiteensis*, which also had longer and narrower incisive foramina, a narrower palate and mesopterygoid fossa, and a rather shallower rostrum than *R. c. cariri*.

Principal components analysis reflected the craniometric distinctness of the four samples. In an analysis of all valid specimens together, a plot of specimen scores on the third principal component (PC3) against the second (Fig.1) could

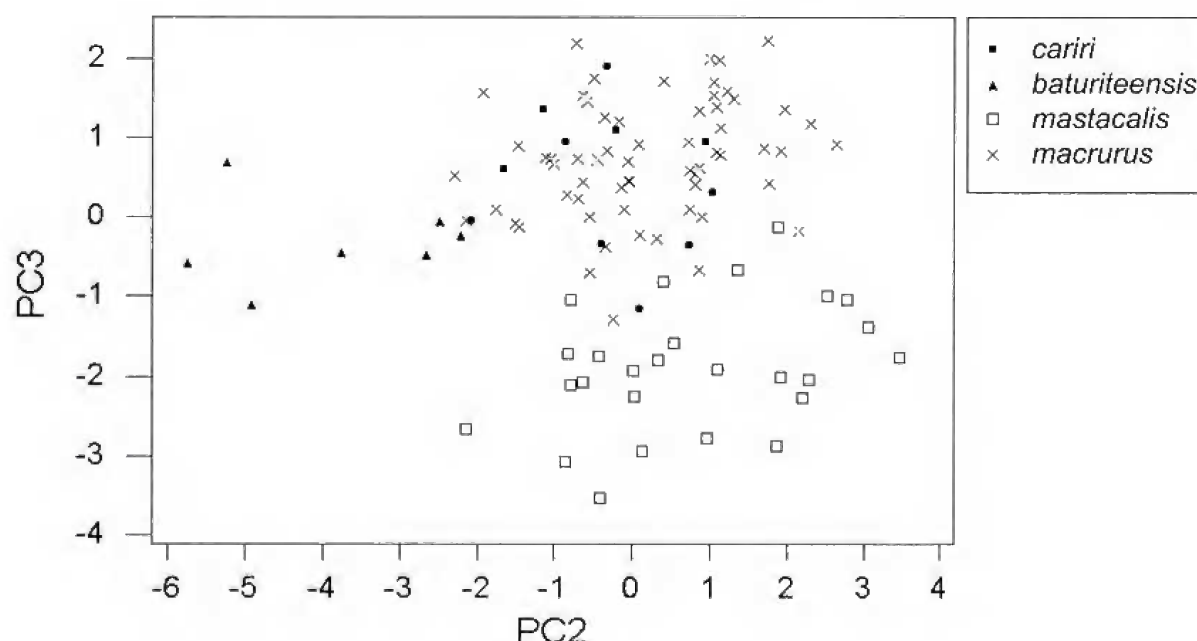


Fig.1- Principal components analysis, using 30 variables, of all analysable specimens: *Rhipidomys cariri cariri* ssp.nov. ($n = 11$), *R. c. baturiteensis* ssp.nov. ($n = 7$), *R. macrurus* from Serra de Ibiapaba, Ceará ($n = 63$), and *R. mastacalis* from Pernambuco ($n = 26$). Plot of scores on the second and third components.

be divided into three main areas, occupied respectively by the *R. c. baturiteensis* sample, the *R. mastacalis* sample, and the *R. c. cariri* plus *R. macrurus* samples. *Rhipidomys c. baturiteensis* was separated from the remainder mainly along the PC2 axis, while *R. mastacalis* clustered apart mainly on PC3, with little overlap in each case. The size of the coefficients on the second latent vector (see table 2 for all latent vectors discussed) suggested that *R. c. baturiteensis* was distinguished by its larger molars and bullae compared with incisive foramen breadth and rostral height. The third latent vector was more complex to interpret, with large positive loadings particularly for bullar dimensions and a large negative one for palatal bridge length; since the *R. mastacalis* specimens clustered at the negative end of the component, they might be expected to have a relatively longer palatal bridge and/or smaller bullae than the rest.

Clearer separations resulted when only two or three groups were included in the dataset analysed. The large series of *R. macrurus* and *R. mastacalis*, for instance, when analysed together, formed separate ellipsoid clusters in a plot of PC3 against PC2. The second latent vector contrasted molar and palatal bridge lengths with bullar dimensions and incisive foramina length, *R. mastacalis* having relatively smaller bullae, a longer palatal bridge and shorter incisive foramina on average than *R. macrurus*. The third latent vector emphasised a combination of bullar plus molar variables against a collection of breadth variables from the central portion of the skull (IFB, IOB, MFB, PB3), suggesting that in *R. mastacalis* that region might be broader for a given molar/bullar size than in *R. macrurus* skulls.

Separate analyses of *R. c. baturiteensis* with *R. macrurus* and of *R. c. baturiteensis* with *R. mastacalis* resulted in clearly distinct clusters in plots of PC2 against PC1. In each case, as in the analysis illustrated in figure 1, virtually all the separation was along the second component axis and was due to the larger molars and bullae of *R. c. baturiteensis* in contrast to variables that showed no appreciable difference between the samples, such as rostral height. *Rhipidomys c. baturiteensis* also clustered towards the more negative end of the PC1 axis in each case, whereas the *R. macrurus* and *R. mastacalis* specimens spanned the whole range of values. The corresponding latent vector consisted of large negative loadings for major skull dimensions with smaller, also negative, contributions from

basicranial and molar variables. It could thus be interpreted as a general (negative) skull size component (REYMENT, BLACKITH & CAMPBELL, 1986). *Rhipidomys c. baturiteensis* skulls therefore lay at the larger end of the size range included in the analysis.

When the *R. c. baturiteensis* and *R. c. cariri* specimens were analysed together, the two groups occupied separate but contiguous areas in plots of PC2 against PC1 (Fig.2) and of PC4 against PC2. *Rhipidomys c. baturiteensis* tended to score higher than *R. c. cariri* on all three components. The first latent vector contained large positive loadings for the molar rows and most skull dimensions except for variables concentrated in the central portion of the skull, which were much less important. The second contrasted these (palatal breadth at M1, temporal fossa length, mesopterygoid fossa breadth and interorbital breadth, all with large negative coefficients) with molar size (positive), while the fourth latent vector contrasted interorbital breadth (negative loadings) with length variables (nasal, palatal bridge and temporal fossa – positive). These results suggest that the central portion of the skull in *R. c. cariri* might be broader, whereas *R. c. baturiteensis* has larger molars and a longer, more slender rostral part. Indeed, the raw skull measurements show that, on average, *R. c. cariri* has a broader palatal bridge and mesopterygoid fossa, while *R. c. baturiteensis* has longer and broader molars, and longer and more slender incisive foramina.

The fact that the *R. c. cariri* sample had a preponderance of males (8 out of 11) and an average dental age class of 3.3, compared with only 3 males out of 7 and an average dental age class of 2.6 in the *R. c. baturiteensis* sample, might at first sight suggest that the differences between the groups could be due to sexual and ontogenetic variation. It is significant, however, that molar dimensions and variables located in the central portion of the *Rhipidomys* skull are less influenced by sex and age than most longitudinal measurements, which tend to be larger in males and older specimens (TRIBE, 1996). Since the latent vectors suggest that relatively larger longitudinal measurements characterise *R. c. baturiteensis* whereas *R. c. cariri* has relatively larger central skull dimensions (and this is borne out by the raw data), the differences cannot be attributed solely to the sex/age composition of the samples.

When *Rhipidomys c. cariri* and *R. mastacalis* were analysed together, a plot of scores on the first two principal components placed them in two distinct but contiguous clusters. The first component showed that the *R. c. cariri* specimens were larger on average, while the second suggested they had larger molars and bullae, a shorter palate and a relatively shallower rostrum than *R. mastacalis*.

Table 1 A. Descriptive statistics for a selection of variables and ratios of untransformed data for four *Rhipidomys* samples: means and standard deviations (in mm), and number of specimens (n). Table 1 B. Probabilities (p) calculated from Student's t-tests for the equality of population means. p values ≤ 0.05 but >0.01 (■) indicate a remote probability, and those ≤ 0.01 (□) indicate a very remote probability, that the populations in question have equal means.

A. DESCRIPTIVE STATISTICS														
TAXON SAMPLE	VARIABLE OR RATIO	ONL	MRC	M1B	IFL	IFB	MFB	BW	IOB	RL/ ONL	PBL/ MRC	PB1/ PBL	RH/ RL	IFB/ IFL
<i>R. c. cariri</i> (Crato)	mean	35.733	5.185	1.425	7.117	2.907	2.413	4.468	5.468	0.308	0.944	0.665	0.596	0.409
	s.d.	0.709	0.135	0.035	0.305	0.132	0.190	0.138	0.211	0.007	0.058	0.041	0.022	0.016
	n	9	23	23	11	11	11	8	11	9	11	11	11	11
<i>R. c. baturiteensis</i> (Pacoti)	mean	35.223	5.447	1.507	7.593	2.727	2.090	4.520	5.321	0.315	0.942	0.592	0.565	0.359
	s.d.	1.176	0.121	0.048	0.314	0.117	0.160	0.235	0.214	0.006	0.036	0.036	0.036	0.016
	n	7	15	15	7	7	7	7	7	7	7	7	7	7
<i>R. macrurus</i> (Serra de Ibiapaba)	mean	34.021	4.992	1.393	6.951	2.757	2.149	4.254	5.260	0.298	0.978	0.633	0.635	0.397
	s.d.	1.580	0.144	0.054	0.387	0.169	0.184	0.124	0.266	0.008	0.045	0.045	0.023	0.027
	n	63	108	119	67	67	67	66	67	63	67	67	64	67
<i>R. mastacalis</i> (Pernambuco)	mean	33.674	4.984	1.375	6.637	2.783	2.244	4.030	5.446	0.300	1.037	0.580	0.629	0.419
	s.d.	1.660	0.130	0.044	0.400	0.219	0.212	0.129	0.255	0.008	0.059	0.049	0.031	0.024
	n	27	37	40	27	27	27	27	27	27	25	26	27	27
B. STUDENT'S t-TESTS: VALUES OF p														
POPULATIONS COMPARED	VARIABLE OR RATIO	ONL	MRC	M1B	IFL	IFB	MFB	BW	IOB	RL/ ONL	PBL/ MRC	PB1/ PBL	RH/ RL	IFB/ IFL
<i>R. c. cariri</i> - <i>R. c. baturiteensis</i>		0.299	□0.000	□0.000	□0.006	□0.009	□0.002	0.601	0.171	■0.041	0.941	□0.002	■0.033	□0.000
<i>R. c. cariri</i> - <i>R. macrurus</i>		□0.002	□0.000	□0.007	0.170	□0.007	□0.000	□0.000	■0.014	□0.000	■0.026	■0.026	□0.000	0.209
<i>R. c. cariri</i> - <i>R. mastacalis</i>		□0.001	□0.000	□0.000	□0.001	0.089	■0.028	□0.000	0.803	■0.011	□0.000	□0.000	□0.003	0.175
<i>R. c. baturiteensis</i> - <i>R. macrurus</i>		0.051	□0.000	□0.000	□0.000	0.618	0.419	□0.000	0.528	□0.000	■0.042	■0.041	□0.000	□0.000
<i>R. c. baturiteensis</i> - <i>R. mastacalis</i>		■0.027	□0.000	□0.000	□0.000	0.523	0.084	□0.000	0.243	□0.000	□0.000	0.525	□0.000	□0.000
<i>R. macrurus</i> - <i>R. mastacalis</i>		0.368	0.771	0.057	□0.001	0.585	■0.031	□0.000	□0.002	0.233	□0.000	□0.000	0.312	□0.001

(ONL) occipito-nasal length, (MRC) upper molar row – crown length, (M1B) 1st upper molar breadth, (IFL) incisive foramen length, (IFB) incisive foramen breadth, (MFB) mesopterygoid fossa breadth, (BW) bullar width, (IOB) interorbital breadth, (RL) rostral length, (PBL) palatal bridge length, (PB1) palatal breadth at M1, (RH) rostral height.

An analysis of *R. c. cariri* with all the *R. macrurus* specimens, however, failed to provide complete separation of the two groups. In case the different sizes and sex/age compositions of the samples might be affecting the analysis, the 11 *R. c. cariri* specimens were then analysed simultaneously with subsets of 11 *R. macrurus* and 11 *R. mastacalis* specimens, each of which matched the composition of the *R. c. cariri* sample as closely as possible in terms of sex and dental age class. Where more specimens were available in a particular sex/age category than were required for the subset, the appropriate number of individuals was selected at random. In the resulting analysis, a plot of scores on PC2 and PC3 provided good separation of the three groups, with minimal overlap (Fig.3). *Rhipidomys c. cariri* was distinguished almost entirely along the second component axis on the basis of its larger molars and bullae and broader palate and mesopterygoid fossa, and its relatively shallower rostrum and shorter palatal bridge.

The results of both univariate and multivariate analyses thus demonstrate the distinctness of the four geographical series of *Rhipidomys* specimens examined, confirming the morphologically based taxonomic hypothesis that they belong to four distinct taxa. Most of the variation between the four groups seems to be concentrated in dimensions of the molars, bullae, palate, incisive foramina, and rostrum. The larger molars and

bullae of *Rhipidomys cariri* as a species are particularly important in distinguishing it from its neighbours, while at a subspecies level *R. c. baturiteensis* differs in its narrower palate and longer, more slender rostrum from *R. c. cariri*. It is unfortunate, however, that the overlap between the four taxa in their ranges of measurements means that there is no variable or ratio that could serve as an unambiguous marker to identify a specimen from its skull. *R. cariri* therefore has to be determined on the basis of a somewhat subjective assessment of skin and skull characters.

Rhipidomys cariri sp.nov.

Rhipidomys cearanus – MOOJEN, 1943 (not *Rhipidomys cearanus* Thomas, 1910).

Holochilus sciureus – FREITAS, 1957 (part; not *Holochilus sciureus* Wagner, 1842).

Rhipidomys mastacalis – MARES *et al.*, 1981 (part; not *Mus mastacalis* Lund, 1840).

Holotype – BRAZIL - CEARÁ: Crato (07°14'S 39°23'W), Sítio Caiana; MN 10170; adult ♂; collected by Batista for the Serviço Nacional de Peste on 20 August 1946, in a palm tree; field number 3. Condition: round study skin in good condition; cleaned skull and mandible (rami joined at symphysis), slightly damaged (left pterygoid process separated; left jugal and both lacrimals missing, left nasal tip chipped).

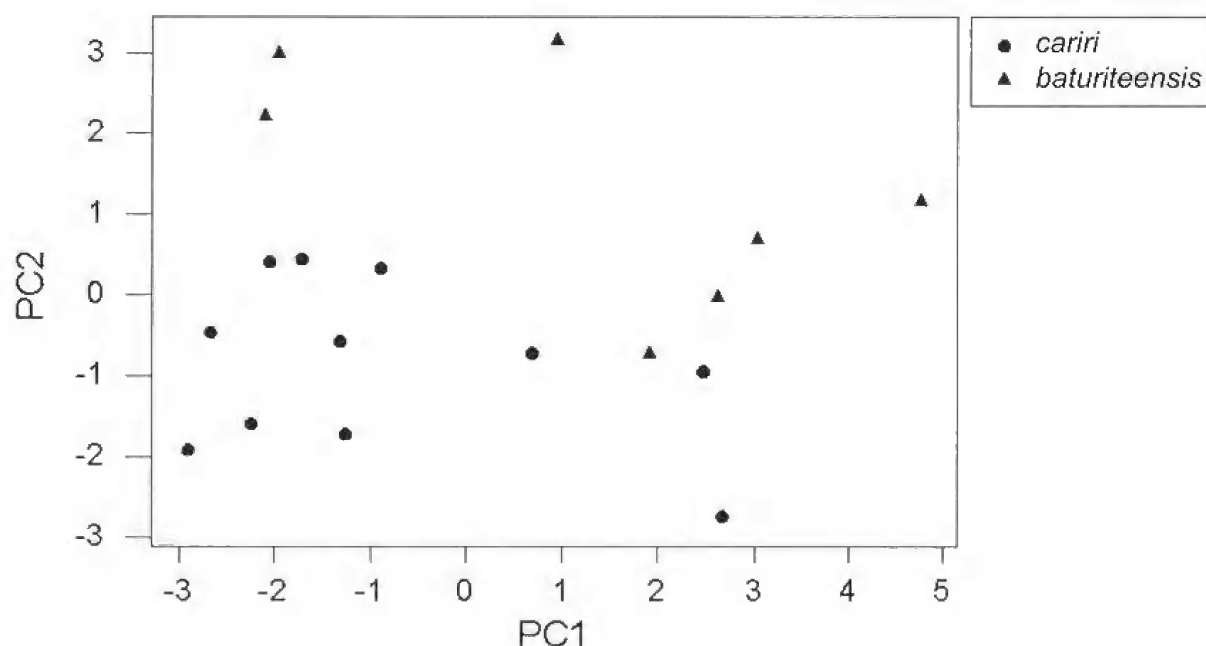


Fig.2- Principal components analysis of all analysable specimens of *Rhipidomys cariri cariri* ssp.nov. (n = 11) and *R. c. baturiteensis* ssp.nov. (n = 7), using 15 variables. Plot of scores on the first and second components.

Table 2. Selected latent vectors from principal components analyses discussed in the text (coefficients rounded to two decimal places for clarity).

SAMPLES ANALYSED	<i>cc-cb-mc-ms</i>		<i>mc-ms</i>		<i>cb-mc</i>		<i>cb-ms</i>		<i>cc-cb</i>			<i>cc-mc</i>		<i>cc-mc-ms</i>	
NO OF SPECIMENS	107		89		70		33		18			37		33	
NO OF VARIABLES	30		30		30		30		15			30		30	
LATENT VECTOR	LV2 LV3		LV2 LV3		LV1 LV2		LV1 LV2		LV1 LV2 LV4			LV1 LV2		LV2 LV3	
VARIABLE															
ONL	0.04	0.03	-0.02	-0.02	-0.24	-0.08	-0.23	0.05				-0.24	0.01	0.00	-0.04
CIL	0.06	0.05	-0.05	-0.01	-0.24	-0.09	-0.24	0.05				-0.24	0.03	0.04	-0.05
PL	0.08	-0.15	0.08	0.12	-0.23	-0.04	-0.23	0.10	0.34	-0.15	0.21	-0.21	0.22	0.17	0.14
PPL	0.07	0.21	-0.17	-0.10	-0.21	-0.17	-0.22	0.04				-0.22	-0.05	0.00	-0.17
MRC	-0.42	-0.18	0.36	-0.39	-0.16	0.38	-0.15	-0.35	0.37	0.19	0.00	-0.13	-0.40	-0.45	0.15
MRA	-0.36	-0.30	0.44	-0.24	-0.16	0.38	-0.15	-0.31				-0.13	-0.31	-0.43	0.23
M1B	-0.36	0.00	0.10	-0.35	-0.09	0.36	-0.16	-0.27				-0.14	-0.18	-0.18	-0.15
PBL	0.01	-0.44	0.31	0.08	-0.17	0.06	-0.09	0.03	0.23	-0.06	0.36	-0.01	0.32	0.19	0.38
TFL	0.03	-0.07	0.06	0.01	-0.21	0.00	-0.22	0.07	0.11	-0.41	0.35	-0.21	0.06	0.01	0.11
DL	0.10	0.06	-0.12	0.07	-0.22	-0.09	-0.23	0.06				-0.22	0.18	0.22	-0.05
IFL	-0.04	0.23	-0.21	-0.05	-0.21	0.01	-0.20	-0.09				-0.21	-0.08	0.04	-0.25
IFB	0.22	0.02	-0.05	0.28	-0.09	-0.21	-0.13	0.27				-0.19	0.04	-0.02	-0.11
PB1	0.11	0.10	-0.07	0.04	-0.12	-0.17	-0.12	0.14	0.09	-0.53	0.08	-0.16	-0.13	-0.20	0.00
PB3	0.11	-0.14	0.10	0.19	-0.13	-0.11	-0.07	0.16				-0.12	-0.08	-0.20	0.20
MFB	0.18	-0.09	0.12	0.21	-0.08	-0.15	-0.06	0.33	-0.13	-0.39	-0.10	-0.15	-0.04	-0.19	-0.01
BIT	0.10	-0.09	0.05	0.13	-0.17	-0.07	-0.19	0.12				-0.17	0.27	0.18	0.09
BW	-0.26	0.34	-0.31	-0.33	-0.14	0.22	-0.16	-0.30	0.27	0.14	-0.14	-0.16	-0.32	-0.25	-0.30
BL	-0.34	0.39	-0.26	-0.46	-0.12	0.30	-0.10	-0.36				-0.09	-0.43	-0.29	-0.37
BCB	-0.07	-0.05	0.07	-0.05	-0.20	0.08	-0.21	-0.03	0.29	0.09	-0.10	-0.21	-0.02	-0.06	0.08
SH	0.10	0.02	-0.04	0.01	-0.21	-0.13	-0.22	0.08	0.34	-0.20	-0.03	-0.22	0.13	0.13	0.02
RH	0.21	0.03	-0.05	0.02	-0.18	-0.24	-0.16	0.23				-0.20	0.21	0.20	0.09
RB	0.01	-0.10	0.10	0.09	-0.19	-0.03	-0.21	0.03	0.25	-0.19	-0.20	-0.22	-0.05	-0.14	0.17
RL	-0.02	0.04	-0.04	0.02	-0.23	0.03	-0.22	-0.03				-0.22	-0.01	-0.04	-0.14
NL	0.07	0.03	-0.04	0.03	-0.21	-0.06	-0.20	0.07	0.25	-0.02	0.40	-0.18	0.18	0.15	-0.06
ZPL	-0.04	0.20	-0.24	-0.03	-0.17	0.05	-0.21	-0.07	0.35	0.14	-0.14	-0.20	0.05	0.05	-0.09
IOB	0.14	-0.28	0.18	0.23	-0.13	-0.12	-0.10	0.20	0.12	-0.30	-0.50	-0.12	0.05	-0.04	0.40
ZB	0.08	-0.02	0.01	0.03	-0.22	-0.11	-0.22	0.08				-0.22	0.04	0.06	0.03
GLM	0.03	0.07	-0.05	-0.03	-0.23	-0.05	-0.22	0.04				-0.22	0.06	0.06	-0.08
MMR	-0.37	-0.28	0.38	-0.23	-0.15	0.38	-0.14	-0.30	0.34	0.31	-0.06	-0.06	-0.11	-0.22	0.30
DR	-0.01	0.09	-0.10	0.00	-0.18	0.00	-0.19	-0.02	0.12	-0.18	-0.43	-0.17	-0.07	-0.05	-0.13

Samples analysed: (cc) *Rhipidomys cariri cariri*, (cb) *R. c. baturiteensis*, (mc) *R. macrurus*, (ms) *R. mastacalis*. See the text for the abbreviations of the variables.

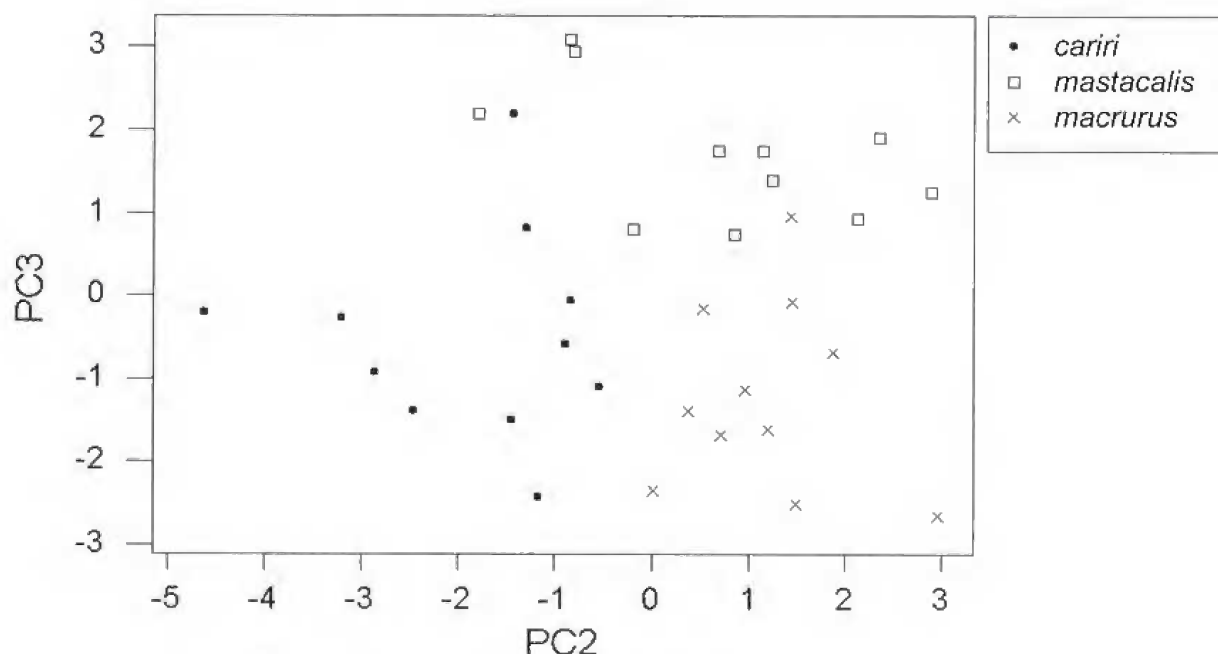


Fig.3- Principal components analysis, using 30 variables, of all analysable *Rhipidomys cariri cariri* ssp.nov. (n = 11) and an equal number each of *R. mastacalis* and *R. macrurus* matching the *R. c. cariri* sample in terms of sex and dental age class. Plot of scores on the second and third components.

Diagnosis – Moderately large *Rhipidomys* specimens with conspicuously agouti, yellowish-grey-brown dorsal pelage and cream underparts; ventral pelage rather woolly in texture; tail longer than head and body, with short to medium-length pencil; hind foot large, broad, with short toes; ears large; vibrissae very long and thick. Skull large and robust, with well-developed supraorbital ridges and broad occiput; palatal bridge very short; bullae and molars moderately large. Carotid circulatory pattern derived (VOSS, 1988: “pattern 3”).

Description – Moderate to large-bodied rats, with adult head-and-body length usually 130-160mm, the largest in the sample being 190mm; tail length equals 110-140% of head-and-body length (Fig.4). Dorsal pelage is yellowish-grey-brown, sometimes a little greyer, sometimes a little redder, but always with conspicuous flecking from the dark guard hairs and dark tips to the body hairs. Dorsal body hairs have mid-grey bases (about 62% of the hair length), an orange subterminal band (about 29%) and a dark tip (8-9%). The ventral pelage is white or pale cream in appearance; some specimens have pale to mid-grey hair bases especially towards the sides and occasionally (as in the holotype) right across the abdomen, as well as in a midline pectoral spot. The pelage texture is slightly coarse and woolly, especially on the ventral surface.

Females have six mammae, as in all *Rhipidomys*. The tail is uniformly coloured, varying among specimens from pale to rather dark; the tail hairs are dark and short (1-2mm) especially along the proximal half of the tail, but may be rather longer at the tip forming a terminal tuft or pencil up to 15mm in length (Fig.4a, c). The hind foot is broad and relatively long compared with other *Rhipidomys* of similar size, measuring 27-30mm including the claw; unfortunately, the collectors’ measurements as given on the specimen labels and SNP record cards for this locality are of little use (they were taken to the nearest centimetre), and the feet of some specimens were deformed too much on drying to be remeasured accurately. The dark patch on the dorsal surface of the metatarsals varies from narrow to broad, but is often poorly defined; the ungual tufts are usually approximately the same length as the claws. The ears seem to be larger in area than in other eastern Brazilian species, although they are barely a millimetre longer on average. The mystacial vibrissae are long (> 50mm) and coarse; genal and supraorbital vibrissae are sparse.

The skull (Figs.5-7, a-b) is large and robust with well-developed, straight supraorbital ridges diverging from the front of the interorbital region. The rostrum is moderately long and the zygomatic

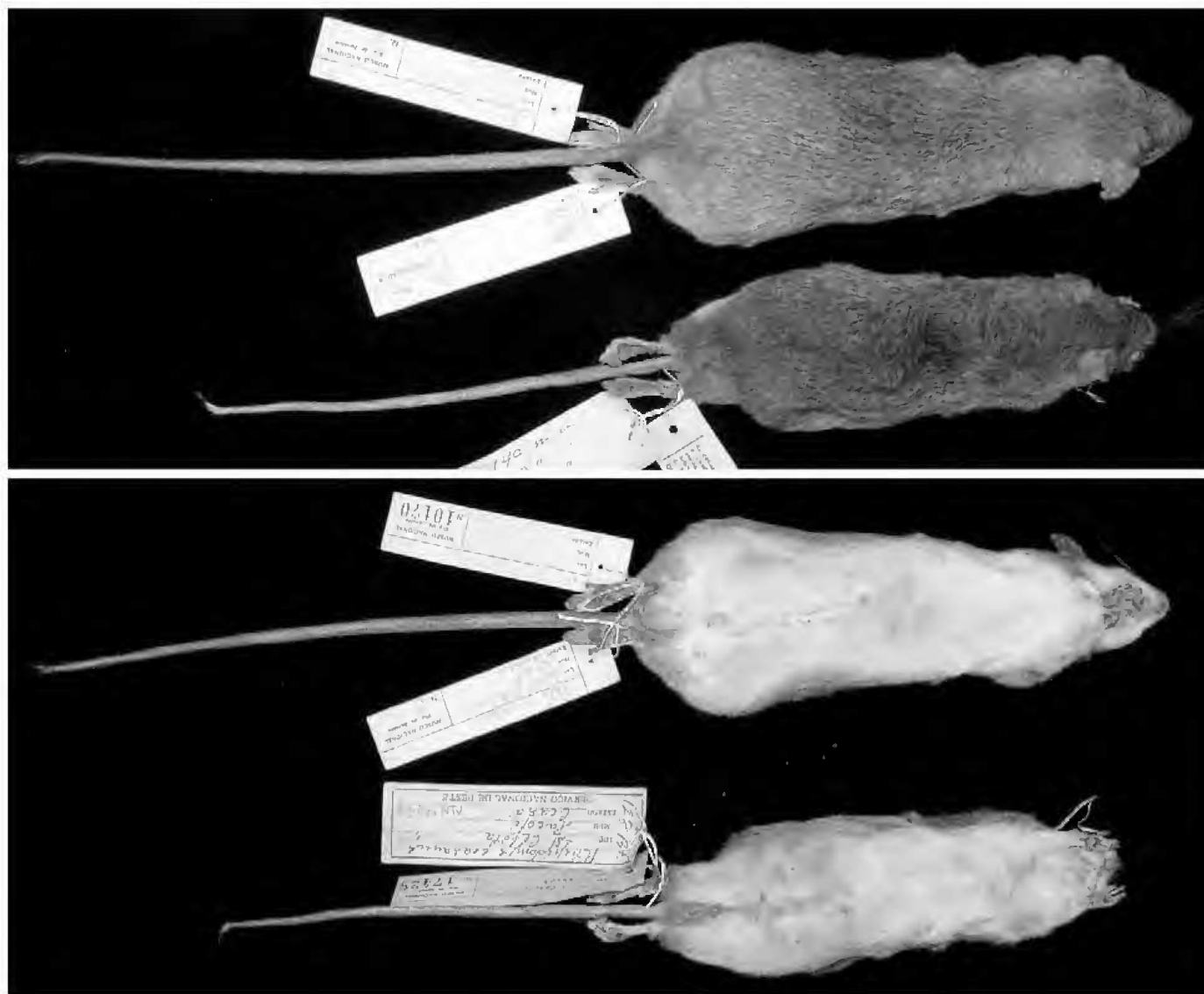


Fig.4- Dorsal and ventral views of skins of *Rhipidomys cariri* sp.nov. Upper specimen in each pair: *R. cariri cariri* ssp.nov. holotype, adult ♂, MN 10170; lower specimen: *R. cariri baturiteensis* ssp.nov. holotype, adult ♀, MN 17428.

plate broad, generally with a shallow zygomatic notch visible in dorsal view. The braincase is large and rather angular rather than rounded, with a broad occiput relative to the greatest breadth across the squamosals; the lateral process of the parietal (the part of the parietal extending below the parietal ridge) is rectangular; the hamular process of the squamosal is long and almost horizontal. The roughly elliptical incisive foramina terminate between the anterior roots of the first molars while the mesopterygoid fossa penetrates between the posterior roots of the third molars, making the palatal bridge shorter than the molar row. Sphenopalatine vacuities are absent. The bullae are relatively large for the genus and slightly

inflated. The carotid circulation pattern is derived (VOSS, 1988: "pattern 3"), with a small stapelial foramen, no translucent internal groove across the squamosal and alisphenoid, and no sphenofrontal foramen.

The upper incisors are robust and more opisthodont than in most *Rhipidomys*. The molars are moderately large for *Rhipidomys* from eastern Brazil (Tab.1, MRC). The first upper and lower molars (M1, m1) have a well-defined antero-medial flexus/flexid; oblique paralophules are present in M1-3; M3 is not greatly reduced in size and occlusal structure.

Comparisons – External and cranial characters

serve to distinguish *R. cariri* from the nearest *Rhipidomys* to the east and west, *R. mastacalis* and *R. macrurus* respectively. The body size of *R. cariri* is larger for equivalently aged specimens, the hind foot is longer and broader, and the mystacial vibrissae are much longer and coarser. The dorsal colour is greyer with a stronger agouti effect (*R. mastacalis* from Pernambuco tends to be a more intense red, and *R. macrurus* from the Serra de Ibiapaba in western Ceará is browner), and the ventral pelage tends to be a little woolly rather than sleek. *Rhipidomys cariri* skulls are generally larger and more robust than all but the oldest *R. macrurus* and *R. mastacalis* (Figs.5-7); in these, however, the zygomatic arches tend to bow outwards so that the greatest breadth lies across the jugals, whereas in *R. cariri* the arches tend to converge forwards from a point on the zygomatic process of the squamosal close to the root. In *R. cariri* the third upper molar is less reduced.

In pelage colour and texture *R. cariri* somewhat resembles *R. leucodactylus*, a species found throughout much of the Amazon basin; *R. leucodactylus* is larger, however, with a hind foot length of at least 32mm, and has considerably larger teeth, its molar row length being in excess of 6mm.

Distribution – Known from the vicinity of Crato, in the large mesic enclave of the Cariri, southern Ceará State, NE Brazil. The specimens were misidentified by SNP personnel in the Crato district as *Holochilus sciureus* and were tallied as such by Freitas in his table of animals caught between 1952 and 1955 (FREITAS, 1957, Tab.1); the Museu Nacional collections demonstrate that no *Holochilus* specimens were in fact taken at Crato. Specimens from the Baturité massif in northern Ceará are described below as a distinct subspecies of *R. cariri*.

Ecological notes – Specimen labels indicate that nine of the Crato specimens were taken in fields, five in palms and two in trees (presumably broadleaf). The SNP individual record cards list the crops grown on the farms where they were caught (rice, beans, maize, manioc, sugarcane) but do not specify whether or not the specimen was found in any one of them. The cards also show that soils varied from sandy and stony to 'black earth'; at some sites rivers were permanent, at others intermittent.

Local names – Names given by collectors on specimen labels are *rato guagipó* and *rato palmeira* (palm rat).

Etymology – The specific epithet refers to the Cariris, a group of indigenous peoples in north-eastern Brazil, whose name is attached to the mesic enclave in southern Ceará where the nominotypical subspecies was collected. Grammatically, *cariri* is treated as a noun in apposition to the genus name, in the nominative case. It is pronounced with the stress on the last syllable (ka-ree-REE).

Material examined – BRAZIL - CEARÁ: Crato (07°14'S 39°23'W, includes Sítio Arisco, Sítio Baixa do Maracujá, Sítio Belo Horizonte, Sítio Caiana, Sítio Grangeiro, Sítio Passagem 1^a, Sítio Passagem 2^a, Sítio Recreio 1^o): MN 1530, 10170 (holotype), 17298, 17299, 17347, 17348, 17349, 17351, 17353, 17378, 17379, 17380, 17417 to 17423, 30012, 30013; KU 27308; USNM 304587, 304588. Total: 24.

Rhipidomys cariri baturiteensis ssp. nov.

Rhipidomys cearanus – FREITAS, 1957 (part; not *Rhipidomys cearanus* Thomas, 1910).

Holotype – BRAZIL - CEARÁ: Pacoti (04°13'S 38°56'W), Sítio Cebola; MN 17428; adult ♀, collected by Mario Pereira for the Serviço Nacional de Peste on 25 July 1953, in a coffee plantation; field number Bt128; pregnant with four embryos. Condition: round study skin in good condition; cleaned skull and mandible (rami separated at symphysis), slightly damaged (tip of left pterygoid process broken; left zygomatic arch split; left bulla glued out of position).

Diagnosis – The tail has relatively short hairs on its distal half and the tail pencil is short; the skull has a short and relatively narrow palatal bridge; and the molars are large and broad.

Description – The dorsal pelage of the holotype of *Rhipidomys cariri baturiteensis* is rather redder-brown than in the nominotypical subspecies *R. c. cariri*, but other specimens are more yellowish-grey-brown, all conspicuously agouti. The ventral pelage is white or pale cream to the hair bases; grey bases only occur ventrally at the extreme sides of the abdomen and in the pectoral spot. The tail hairs are shorter than in *R. c. cariri*, especially along the distal half of the tail, and the pencil extends only a few millimetres beyond the tail tip (Fig.4b, d).

The rostrum is longer compared with skull length, and the incisive foramina are notably more slender than in *R. c. cariri* (Tab.1, ratios RL/ONL and IFB/IFL). The zygomatic plate is broad. The palatal bridge is shorter than the molar row but narrower than in *R. c. cariri* (Tab.1, ratio PB1/PBL); the mesopterygoid

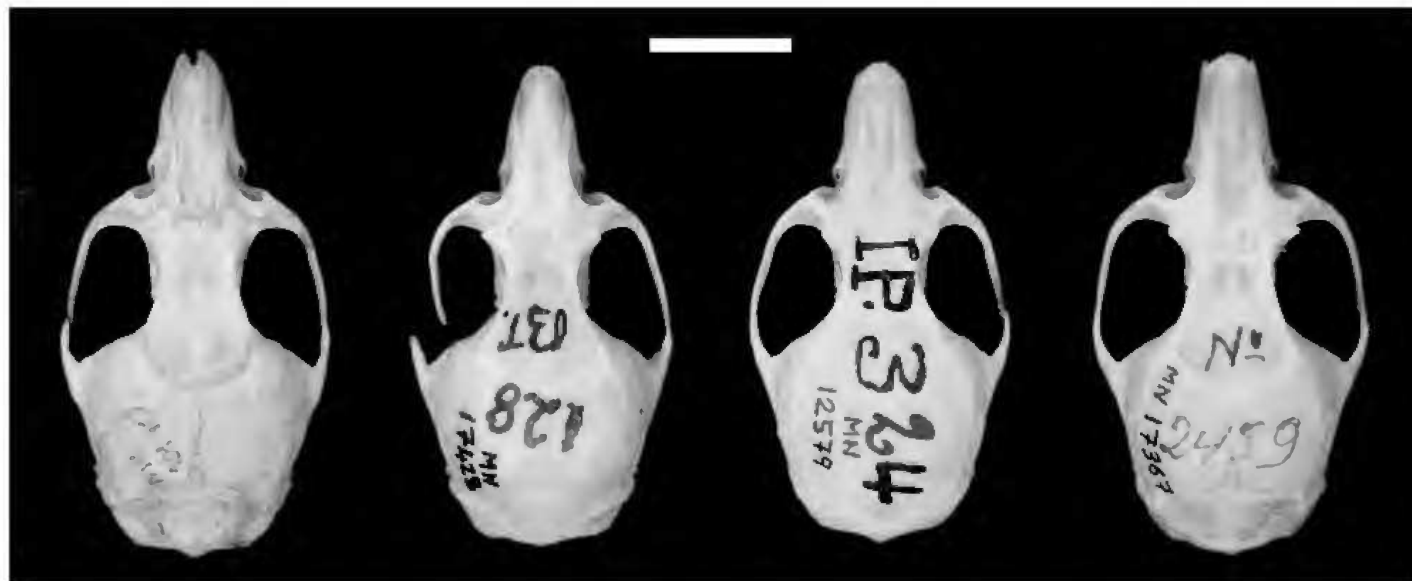


Fig.5- Dorsal view of skulls of *Rhipidomys* from north-eastern Brazil. From left to right: *R. cariri cariri* ssp.nov. holotype, adult ♂, MN 10170; *R. cariri baturiteensis* ssp.nov. holotype, adult ♀, MN 17428; *R. macrurus*, adult ♀, MN 12579; *R. mastacalis*, adult ♂, MN 17367. Scale bar = 10mm.

fossa is also narrower. The molars are larger than in *R. c. cariri* on average (Tab.1, MRC), although not in the holotype, and M1 is significantly broader (Tab.1, M1B). In the upper molars, particularly M2, the hypoflexus often penetrates into the median mure, almost meeting the inner tip of the mesoflexus.

Distribution – Known only from the vicinity of Pacoti, in the isolated mesic enclave of the Serra de Baturité massif, northern Ceará State, NE Brazil, some 330km north of Crato, the type locality of *Rhipidomys cariri*.

Ecological notes – Specimen labels indicate that 12 specimens were taken in sugar cane fields, two in coffee plantations, two in second-growth forest and one in a quarry. Two females (the holotype and MN 17445) each had four embryos in late July 1953. Six males captured between mid-August and early September 1954 had enlarged testes and one did not.

Etymology and local name – The subspecies is named after the Serra de Baturité, an isolated massif in northern Ceará where it was collected, with the suffix *-ensis* denoting provenance; the two 'e's in the epithet *baturiteensis* should therefore be pronounced separately. Local name given by collectors on the specimen labels: *rato de cana* (sugar cane rat).

Material examined – BRAZIL - CEARÁ: Pacoti (04°13'S 38°56'W, includes Sítio Cebola, Sítio Ladeira, Sítio Ouro, Sítio Pirajá, Sítio Santa Rosa): MN 17373, 17428 (holotype), 17431, 17440 to 17446, 30005 to 30011. Total: 17.

DISCUSSION

Rhipidomys cariri sp.nov. is known only from two isolated areas of mesophytic forest, or *brejos*, within the xerophytic *caatinga* domain of north-eastern Brazil. Although at present there are no mesic corridors linking these habitats with either the Atlantic forest to the east or the Amazon forest to the west, it has long been hypothesised that such connections existed in the past, based on the presence in the *brejos* of many plant species also found in those larger forest systems (e.g., RIZZINI, 1963; ANDRADE-LIMA, 1982). Pollen from swamp or lake-bed cores taken at localities currently occupied by Amazon forest (Carajás, Pará) and cerrado (Salitre de Minas, Minas Gerais) shows that the predominant vegetation types fluctuated several times during the late Pleistocene and Holocene: mesophytic floras alternated with xerophytic ones that expanded in approximate synchrony with the temperature and rainfall minima of the Northern Hemisphere Late Glacial (ABSY *et al.*, 1991; LEDRU, 1993). Even in the driest periods, however, mesic areas dependent on orographic precipitation are unlikely to have been severely affected (CLAPPERTON, 1993); the Baturité *brejo* comes into this category. Similarly, since the humidity of the Cariri *brejo* is due to the permanent springs that emerge along the northern and eastern face of the large Araripe mesa, fed from permeable rocks overlying gently sloping impermeable strata within



Fig.6- Ventral view of the same skulls illustrated in figure 2. Scale bar = 10mm.

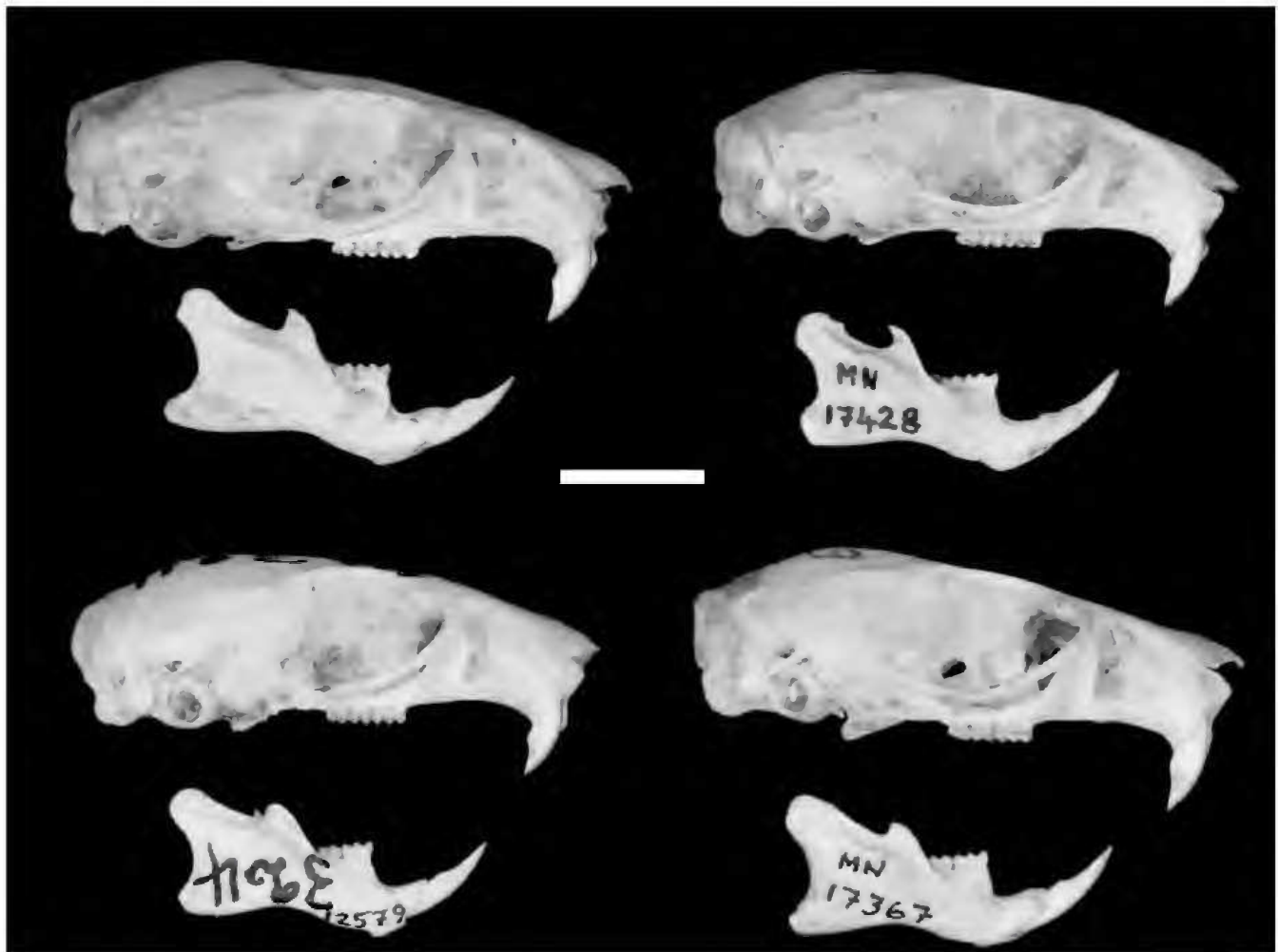


Fig.7- Lateral view of the skulls illustrated in figure 2. Top left: *R. cariri cariri* ssp.nov.; top right: *R. c. baturiteensis* ssp.nov.; bottom left: *R. macrurus*; bottom right: *R. mastacalis*. Scale bar = 10mm.

the mesa (VANZOLINI, 1981; BORGES-NOJOSA & CARAMASCHI, 2003), here too mesic conditions could have continued to provide suitable habitat for *R. cariri* while the remainder of the region experienced even greater aridity than today.

During the wetter phases, forest cover is likely to have been more continuous, linking the present-day *brejos* with both the Amazon and Atlantic forests (VIVO, 1997). At a gallery forest site in the Icatu valley within the *caatinga* in north-western Bahia, pollen evidence points to a humid forest populated with both Amazonian and Atlantic tree species in the period 10 990-10 540 yrs BP, when temperatures were some 5°C cooler than at present (OLIVEIRA, BARRETO & SUGUIO, 1999). Such gallery forests are likely to have persisted as continuous links between the Amazon and Atlantic forests across central Brazil even outside the periods of peak humidity (MEAVE *et al.*, 1991; OLIVEIRA FILHO & RATTER, 1995).

Given the relative recency of the probable connection between the current *brejos* and the more extensive forests to the west and east, it might perhaps be expected that most forest-dwelling small mammal species would be found in all three regions. Even in apparently continuous habitats such as the Amazon and Atlantic forests, however, individual species are not necessarily widespread and phylogeographic patterns within genera vary considerably (PATTON *et al.*, 1997; PATTON, SILVA & MALCOLM, 2000). Divergence estimates based on the mitochondrial cytochrome-*b* gene revealed a complex pattern of relationships among several *Rhipidomys* species in the Atlantic and the Amazonian forests and the region between them, with most genetic divergences dating back to before the Pleistocene (COSTA, 2003). *Rhipidomys cariri* was not represented in the study, unfortunately. These findings preclude a general explanation of diversity based on the Pleistocene forest refuge theory (HAFFER, 1969; VANZOLINI & WILLIAMS, 1970). Although a late Pleistocene/Holocene origin for *R. cariri*, subsequent to the latest isolation of the *brejos* in which it occurs, cannot yet be ruled out, such molecular work does suggest that the species may be much older and survives there as a relict for reasons currently unknown.

Rhipidomys cariri is not the only instance of vertebrate endemism in the *brejos*: a growing number of species restricted to these areas has been described in recent years. They include the forest frogs *Adelophryne baturitensis* and *A. maranguapensis* from the Baturité and Maranguape ranges, respectively (HOOGMOED,

BORGES & CASCON, 1994); the lizards *Mabuya arajara*, from the Cariri, and *Colobosauroides cearensis* and *Leposoma baturitensis*, both found in several *brejos* in Ceará (REBOUÇAS-SPIEKER, 1980; CUNHA, LIMA-VERDE & LIMA, 1991; and RODRIGUES & BORGES, 1997, respectively); and the bird *Antilophia bokermanni*, the Araripe manakin, endemic to the Cariri (COELHO & SILVA, 1998). Apart from *Rhipidomys cariri*, however, no mammal truly endemic to the *brejos* has yet been formally described, although several taxa commonly regarded as local populations of more widespread species may in fact prove to be distinct (OLIVEIRA, GONÇALVES & BONVICINO, 2003).

In the past it was common to refer any specimen of *Rhipidomys* from north-eastern Brazil indiscriminately to *R. cearensis* or *R. mastacalis*, on the assumption that there was a single, widespread species present throughout the region. With the identification of *R. cariri* from the mesic forests isolated within the *caatinga*, and confirmation that *R. macrurus* in western Ceará is distinct from *R. mastacalis* in eastern Pernambuco, three species are now known from the area north of the Rio São Francisco alone. Additional work is still needed in fields such as karyology and DNA research, however, in order to characterise them more fully and to test phylogeographic hypotheses of their relationships and origins. Larger series of specimens suitable for both morphological and molecular work are also needed from forests further south, within and adjacent to the *caatingas* of Bahia, to help elucidate the relationships of these three species with the *Rhipidomys* populations found there.

To summarise, *Rhipidomys* species in north-eastern Brazil are restricted to the mesic *brejos* and, despite the fluctuations in the general climate and vegetation of the region during the Pleistocene and Holocene, these areas are likely to have provided suitable habitat at all times. The Amazon forest, the *brejos* and the Atlantic forest were probably last connected fairly recently, in the early Holocene, but even today spatial continuity of forest does not preclude endemism or restricted ranges, so it is possible that *R. cariri* was confined to this region even when mesophytic forests were more continuous. Indeed, phylogeographic patterns within *Rhipidomys* suggest splitting events that predate the Pleistocene. Further work is therefore needed to show when and how *R. cariri* originated and to clarify its relationships with other *Rhipidomys* taxa.

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